A Multiscale Approach to Capture Patterns and Habitat Correlations of *Peromyscus leucopus* (Rodentia, Muridae)

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ABSTRACT--Capture patterns (presence/absence) of *Peromyscus leucopus* were examined in relation to 12 selected habitat variables at three spatial scales. Trapping was conducted on a 14 X 14 trapping grid established at the Edward J. Meeman Biological Station in southwestern Tennessee. Density of the population was estimated at 18.5 mice per hectare. Twelve habitat variables were collected in three circular plots (1 m^2, 5 m^2, 10 m^2) centered on 60 trap sites (30 trap sites where captures of *P. leucopus* occurred, 30 randomly selected sites where no captures occurred). There was a significant difference among spatial scales for six habitat variables. We observed no discernable patterns through principal components analysis for any scale. However, the centroid of the cluster of traps in principal component space shifted from negative to positive as scale increased. Sites where captures occurred and those where no captures occurred were not significantly different at the 1-m^2 scale for any habitat variables. Capture occasions differed significantly for stems 10-15-cm diameter and logs 10-15 cm at the 5-m^2 and 10-m^2 spatial scales, respectively. Our study emphasizes the need for including multiscale assessments of habitat use. Scales might best be selected by assessing the habitat of the study site and the behavior of the species being studied.

The concept of scale, while not a new concept in other disciplines, has only recently been investigated in ecology (Wiens 1989). Levin (1991) stated that because there is an absence of any correct scale at which to investigate a population, a multiscale approach should be taken. Thus, investigations of species relating habitat use to capture success could be affected by the selected scale. Studies relating habitat use to capture success have generally selected a single scale in which to measure the habitat. This scale of habitat assessment is usually based on amount of time spent for amount of data return. Thus, the scale

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selected for habitat assessment might not be representative for the species being investigated or may affect the results of the study (see Levin 1991, Schneider 1994).

The need for a multiscale approach has been demonstrated in several studies of species interactions. Depending on the scale selected, species of marine birds were or were not associated with their prey species (Woodby 1984, Schneider and Piat 1986). Least flycatchers (*Empidonax minimus*) and redstarts (*Setophaga ruticilla*) had a negative association at small scales and a positive association at larger scales (Sherry and Holmes 1988). Furthermore, behavior of an animal can be affected by the spatial scales at which prey are distributed (Boyd 1996).

Similarly, the association between habitat around a live trap and capture of a selected species lends itself to a multiscale approach. However, capture-recapture studies rarely, if ever, use multiple scales to assess correlations between captures and habitat use. Using capture success is warranted for studies investigating habitat correlations because densities within a habitat can be influenced by factors (e.g. intra- and interspecific interactions) that place subordinates into suboptimal habitats (van Horne 1983). Also, factors such as curiosity of a new object (e.g. a trap) in an area may influence captures (Lackey et al 1985). However, an animal must be present in a habitat for a capture to occur; thus, must use the habitat in some way.

The objective of our study was to investigate the association between captures of *Peromyscus leucopus* and selected habitat variables at three spatial scales centered on location of live traps. Although there is a large amount of literature on *P. leucopus* (see Lackey et al. 1985), to our knowledge, no study has been conducted relating spatial scale to the association between capture success of *P. leucopus* and selected habitat variables.

Peromyscus leucopus is an excellent organism to use in multiscale analyses of correlations between captures and habitat. The species is well studied throughout its range, and habitat affinities are well documented (see Lackey et al. 1985). Because *P. leucopus* is a small mammal, a multiscale study design can be done at small scales, and fine grained changes in habitat are more likely to be exhibited. Previous investigations of habitat affinities of P. *leucopus* (see Lackey et al. 1985) indicate loosely defined associations. However, these loosely defined associations may become more clearly defined with a different or more meaningful choice of scales.

STUDY AREA AND METHODS

The study was conducted at the 252-ha Edward J. Meeman Biological Station (hereafter referred to as the station) located ca. 20 km north of Memphis, Tennessee, (35°20' N, 90°01' W) on the third Chickasaw loess bluff. The station is surrounded on three sides by private lands and on the fourth by the Shelby Forest Wildlife Management Area.

Habitat has been described as a western mixed mesophytic forest (Braun 1950, Miller and Neiswender 1987). Dominant canopy plants are sweet gum (*Liquidambar stryaciflua*), tulip poplar (*Liriodendron tulipifera*), elms (*Ulmus* spp.), oaks (*Quercus* spp.), and hickories (*Carya* spp.). There is an extensive network of grape (*Vitis* spp.) and poison ivy (*Toxicodendron radicans*) vines throughout the canopy. The understory is dominated by spicebush (*Lindera benzoin*). Dominate ground cover species are *Osmorhiza* sp., *Smilacina racemosa, Toxicodendron radicans, Urtica* sp., various woodland grass species, and seedlings of the dominant canopy and understory species. A detailed analysis of the habitat on the station can be found in Ladine (1995).

A 14 X 14 trapping grid was established using folding Sherman live traps (H. B. Sherman Traps, Inc.; Tallahassee, Florida) spaced ca. 10-m apart. Trapping was conducted from 28 January 1995 through 9 February 1995. Traps were baited with oatmeal, left open during the day, and checked at sunrise. Estimation of population size was made using the Schnabel method (Krebs 1989).

Location of the trapping grid was entirely within a mature stand of oak, sweet gum, and tulip poplar trees. The selected location has been shown to be homogenous on the macrohabitat scale (Ladine 1995). Placing the grid in this location avoided potential confoundment during statistical analyses posed by placing traps in differing macrohabitats.

Trap sites were classified according to the occurrence of captures of *P. leucopus*. Trap sites with at least one capture were classified as capture sites. Other sites were classified as no-capture sites. To strengthen the multivariate analyses and remove the possibility of nonorthoganal functions and components (Tabachnick and Fidell 1989), thirty randomly selected no-capture sites were designated for habitat association analyses.

Twelve selected habitat variables (Table 1) were measured at each capture site and at each no-capture sites. All selected habitat variables were measured at each of three spatial scales (1 m^2, 5 m^2, and 10 m^2) in circular plots centered on each trap. These scales were selected following Noon (1981) who suggested that a more homogeneous habitat be sampled more finely than a heterogeneous habitat in order to detect the inherent heterogeneity. Thus, because of the apparent homogeneity of the habitat within the trapping grid (Ladine 1995), these selected scales were used.

All statistical analysis were conducted using Statistical Analysis Systems (SAS Institute 1989). Habitat variables for capture and no-capture sites were compared at each scale with a Kruskal-Wallis test of Chi-square approximation. Selected habitat variables between scales were compared with a Kruskal-Wallis test of Chi-square approximation to test for differences among selected scales. To control for group-wide Type I error, all multiple pairwise comparisons were made using a sequential Bonferroni adjustment (Rice 1989) with initial $\alpha = .05$.

Table 1. Description of selected habitat variables measured at 30 sites with captures of Peromyscus leucopus occurred and 31 sites with no captures of *P. leucopus* for a study in western Tennessee.

Habitat variables	Description
COVER0	Percent green vegetation at ground level
COVER1	Percent green vegetation at 1 m height
COVER2	Percent green vegetation at 2 m height
STEMS0-5	Number of vertical woody stems with diameter <5 cm
STEMS5-10	Number of vertical woody stems with diameter 5-10 cm
STEMS10-15	Number of vertical woody stems with diameter 10-15 cm
STEMS>15	Number of vertical woody stems with diameter >15 cm
LOGS0-5	Number of horizontal woody stems on the ground with diameter of <5 cm
LOGS5-10m	Number of horizontal woody stems on the ground with diameter 5-10 cm
LOGS10-15	Number of horizontal woody stems on the ground with diameter 10-15 cm
LOGS>15	Number of logs at ground level with diameter >15 cm
LITTER	Mean of seven leaf litter depths taken for each scale

The existence of potential patterns at each scale was examined with principal components analysis. Discriminate function analysis was used to further examine the difference between sites with captures and sites where no captures occurred. Initial discriminating variables were selected with stepwise selection discriminate analysis and an initial entry level of significance of P = 0.15. Variables were removed or added to check the selection of variables from the stepwise selection procedure for improvement of the discriminating capabilities of the variables. No addition or subtraction improved the classification for any scale.

RESULTS

Thirty-one *Peromyscus leucopus* were captured 55 times at 30 trap sites. Population size was estimated at 32 mice (range = 26 - 38) with a mean density of 18.5 mice per hectare. Other species, *Tamias striatus* (n = 1), *Blarina carolinensis* (n = 2), *Glaucomys volans*, (n = 7) were captured at eight additional sites. No *P. leucopus* were captured at trap sites where captures of other species occurred.

Table 2. Selected habitat variables ($\underline{x} \pm SD$) and Kruskal-Wallis test (X^2 approximation and probability values) for the differences among three selected scales (1 m^2, 5 m^2, 10 m^2). (See Table 1 for description of the habitat variables.)

Habitat variable	Spatial scale 1 m^2	5 m^2	10 m^2	X^2	*P*
COVER0	2.34 ± 4.20	2.62 ± 4.27	3.06 ± 4.57	2.06	0.3566
COVER1	0.22 ± 1.02	0.60 ± 2.87	0.95 ± 3.81	1.75	0.4171
COVER2	0.44 ± 2.63	0.81 ± 5.15	1.08 ± 5.91	0.56	0.7565
STEMS0-5	4.24 ± 5.24[b] [1]	7.65 ± 8.71[a]	4.03 ± 14.92[ab]	21.56	0.0001
STEMS5-10	0.06 ± 0.24[b]	0.13 ± 0.34	0.31 ± 0.59[b]	8.59	0.0136
STEMS10-15	0.08 ± 0.27	0.13 ± 0.34	0.22 ± 0.42	5.44	0.0657
STEMS>15	0.04 ± 0.21	0.11 ± 0.32	0.22 ± 0.46	7.63	0.0220
LOGS0-5	6.72 ± 7.68[a]	1.42 ± 12.81[a]	18.34 ± 21.31[a]	21.44	0.0001
LOGS5-10	0.24 ± 0.50[b]	0.42 ± 0.71	0.70 ± 1.08[b]	8.07	0.0176
LOGS10-15	0.08 ± 0.37	0.08 ± 0.37	0.27 ± 0.68	8.03	0.0180
LOGS>15	0.08 ± 0.27	0.11 ± 0.36	0.18 ± 0.42	2.27	0.3215
LITTER	46.57 ± 12.78	49.19 ± 11.84	51.12 ± 13.01	4.36	0.1132

[1] Means followed by the same letter are not different ($P > 0.017$) with a Bonferroni adjustment to the initial significance level ($P = 0.05$).

Significant differences among the selected scales were found for STEMS<5, STEMS5-10, STEMS>15, LOGS<5, LOGS5-10, and LOGS10-15 (Table 2). Except for LOGS<5, the 1-m^2 and 5-m^2, scales did not differ significantly for selected variables. The 10-m^2 scale was significantly different from both the 1-m^2 and 5-m^2 scales for all variables exhibiting significant differences between the three scales.

No significant difference was observed between capture and no-capture sites for selected habitat variables at the 1-m^2 scale (Table 3). Except for STEMS10-15, no significant difference was found between capture and no-capture sites for selected habitat variables at the 5-m^2 scale (Table 4). At the 10-m^2 scale, a significant difference was found between capture and no-capture sites for LOGS10-15 (Table 5).

Sites with no captures tended to be centered in the cluster of sites on graphs of principal components for all scales. Outliers from sites where no captures occurred were only observed at the 1-m^2 spatial scale. Percent variation accounted for by the first three principal components for each scale was 42.0% at 1 m^2, 39.5% at 5 m^2, and 45.3% at 10 m^2 . Variables loading on each of the first three principal components varied for each scale. For the 1-m^2 scale, all

Table 3. Selected habitat variables (x ± SD) and Kruskal-Wallis test (χ^2 approximation and probability values) for differences between sites where Peromyscus leucopus were captured and randomly selected sites where no captures occurred for the 1-m^2 scale. (See Table 1 for description of habitat variables. See text for explanation of capture and no-capture sites.)

Habitat variable	Capture	No-Capture	χ^2	P
COVER0	2.50 ± 4.84	2.29 ± 3.68	0.02	0.8841
COVER1	0.13 ± 0.73	0.29 ± 1.19	0.36	0.5507
COVER3	0.07 ± 0.37	0.74 ± 3.51	0.36	0.5507
STEMS0-5	4.63 ± 5.33	4.59 ± 5.57	0.46	0.4995
STEMS5-10	0.03 ± 0.18	0.09 ± 0.29	0.99	0.3210
STEMS10-15	0.13 ± 0.35	0.03 ± 0.17	2.04	0.1536
STEMS>15	0.03± 0.18	0.06 ± 0.24	0.31	0.5766
LOGS0-5	8.13 ± 8.49	5.32 ± 6.51	2.06	0.1512
LOGS5-10	0.17 ± 0.46	0.29 ± 0.52	2.04	0.1532
LOGS10-15	0.13 ± 0.51	0.03 ± 0.17	0.43	0.5128
LOGS>15	0.13 ± 0.35	0.03 ± 0.17	2.04	0.1536
LITTER	49.22 ± 13.52	44.45 ± 11.28	2.10	0.1471

Table 4. Selected habitat variables (x ± SD) and Kruskal-Wallis test (χ^2 approximation and probability values) for differences between sites where Peromyscus leucopus were captured and randomly selected sites where no captures occurred for the 5-m^2 scale. (See Table 1 for description of habitat variables. See text for explanation of capture and no-capture sites.)

Habitat variable	Capture	No capture	χ^2	P
COVER0	2.20 ± 4.63	2.85 ± 3.82	2.02	0.1558
COVER1	0.17 ± 0.65	0.94 ± 3.79	0.22	0.6383
COVER2	0.33 ± 1.09	1.18 ± 6.86	1.02	0.3132
STEMS0-5	8.60 ± 9.35	8.09 ± 9.17	0.32	0.5716
STEMS5-10	0.17 ± 0.38	0.09 ± 0.29	0.64	0.4227
STEMS10-15	0.23 ± 0.43	0.06 ± 0.24	5.32	0.0211
STEMS>15	0.07 ± 0.25	0.15 ± 0.36	1.32	0.2503
LOGS0-5	12.47 ± 14.37	10.38 ± 11.18	0.02	0.8793
LOGS5-10	0.27 ± 0.58	0.56 ± 1.39	3.26	0.0709
LOGS10-15	0.13 ± 0.51	0.03 ± 0.17	0.43	0.5128
LOGS>15	0.17 ± 0.46	0.06 ± 0.24	0.85	0.3565
LITTER	48.80 ± 12.37	49.53 ± 11.34	0.06	0.8118

Table 5. Selected habitat variables (x ± SD) and Kruskal-Wallis test (χ^2 approximation and probability values) for differences between sites where Peromyscus leucopus were captured and randomly selected sites where no captures occurred for the 10-m^2 scale. (See Table 1 for description of habitat variables. See text for explanation of capture and no-capture sites.)

Habitat variable	Capture	No capture	χ^2	P
COVER0	2.53 ± 4.14	3.47 ± 4.86	1.62	0.2033
COVER1	0.47 ± 1.48	1.29 ± 4.93	0.13	0.7152
COVER2	0.60 ± 2.06	1.41 ± 7.72	0.24	0.6275
STEMS0-5	15.43 ± 15.34	15.15 ± 16.54	0.91	0.3395
STEMS5-10	0.33 ± 0.61	0.26 ± 0.57	0.12	0.7298
STEMS10-15	0.30 ± 0.47	0.18 ± 0.39	1.63	0.2015
STEMS>15	0.17 ± 0.38	0.27 ± 0.51	0.83	0.3611
LOGS0-5	20.63 ± 25.15	16.38 ± 17.18	0.02	0.8851
LOGS5-10	0.67 ± 1.09	0.71 ± 1.06	0.28	0.5937
LOGS10-15	0.50 ± 0.90	0.09 ± 0.29	5.97	0.0144
LOGS >15 cm	0.23 ± 0.50	0.12 ± 0.33	0.62	0.4318
LITTER	52.26 ± 13.04	50.65 ± 13.05	0.12	0.7292

percent cover measurements correlated positively along the first principal component. Vertical stems correlated along the second principal component with the two smaller stem categories correlating positively and the larger stem categories correlating negatively. Logs were correlated to the third principal component with all but LOGS>15 correlated positively. For the 5-m² scale, the first principal component was correlated positively to all cover measurements and STEMS0-5, and negatively to STEMS10-15. The second principal component was correlated positively to LOGS0-5 and LOGS5-10. The third principal component was correlated positively to STEMS5-10 and STEMS>15 and LITTER, and correlated negatively to LOGS10-15 and LOGS>15. For the 10-m² scale, the first principal component was correlated positively to STEMS10-15, LOGS0-5, and LITTER, and correlated negatively to COVER0 and COVER1. The second principal component was correlated positively to LOGS5-10, LOGS10-15, and LOGS>15. The third principal component was correlated positively to COVER1 and STEMS5-10, and correlated negatively to STEMS0-5, and STEMS>15.

Correct classification of sites with captures was poor for all scales: 1 m -- 46.7%; 5 m-- 56.7%; 10 m -- 40.0%. Classification of sites where no captures occurred was better at all three scales: 1 m -- 70.0%; 5 m -- 98.3%; 10 m -- 76.7%. Variables selected for discriminating between capture and no-capture sites were different for each scale. LITTER, and LOGS>15 were selected for the 1-m² scale. STEMS10-15, 2 m COVER, and LOGS>15 cm were selected at the 5-m² scale. LOGS10-15, 2 m COVER, STEMS0-5, and LITTER were selected at the 10-m² scale.

DISCUSSION

Members of the genus *Peromyscus* exhibit habitat generality, at least on a local scale, and often occur across a broad range of habitats within a small geographic area (Kirkland 1976, Batzli 1977, Sullivan 1979, Van Horne 1981, Martell 1983, Adler et al. 1984). There are conflicting reports concerning relationship between density of *P. leucopus* and habitat type (Klein 1960, Stickel and Warbach 1960, Getz 1961, Bongiorno and Pearson 1964, Kaufman and Fleharty 1974). Density in our study was within the reported ranges for the species (see Lackey et al. 1985). Findings of our study at the 5-m² scale, in concurrence with Kaufman and Fleharty (1974), suggest a relationship between number of stems 10-15 cm and captures of *P. leucopus*. However, this relationship was not observed at the 10-m² scale. A relationship between logs 10-15 cm and captures of *P. leucopus* was observed at the 10-m² scale. These finding are similar to those of Getz (1961). Although relationships were observed between two of the selected habitat variables and captures of *P. leucopus*, lack of significant relationships between other variables for all scales appears to reflect the habitat generality of the species.

Lack of readily discernable patterns between captures and selected habitat variables could be a reflection of the variables we selected and lack of differences between spatial scales for some variables. There are at least three potential reasons for the lack of a readily discernable pattern between capture and no-capture sites. First, low statistical power might have resulted in the lack of differences observed in our study. However, because of the large amount of variation observed for all means and the finding of significant differences for the larger scales, the lack of differences is most likely not due to low statistical power. Second, captures of *P. leucopus* are often related to factors other than habitat. The species is known to respond to new objects placed within a familiar area (Lackey et al. 1985), and densities have been shown to correlate to food distribution (Getz 1961). Third, the spatial scales selected for study might have been of an incorrect size for ascertaining capture patterns. However, the lack of patterns in our study does not necessarily indicate scale is not important in associating captures of *P. leucopus* with habitat, only that a different scale may be warranted for future studies.

Our study shows at least two potential means by which selection of scale could influence results of a study warranting investigation of potential patterns at each scale. First, significant differences found for some variables suggest difference at the 10-m^2 scale, but not at smaller scales. Second, the differences in the loadings of variables on the principal components axes, differences in variables selected for use in discriminant analysis, and the decrease in outliers as scale increases suggest differences between all of the scales. These differences between scales may potentially have a large effect on the conclusions (see Schneider and Piat 1986, Woodby 1984). For example, our study had inconsequential findings at the 1-m^2 scale; but significant results at the larger scales.

Our data show that, even when using the small scales that we selected, differences in habitat affinities for capture can occur around the same trap site. Because our data were collected in a homogenous habitat over a short period of time, the differences observed in our study concerning correlations between habitat and capture can be attributed to the different scales. While a species may appear to be a habitat generalist with an affinity toward a variety of habitats (e.g. *P. leucopus*), studies incorporating a multiscale approach may indicate a narrower range of optimal habitat affinities. Thus, studies assessing habitat use should incorporate analyses at multiple scales. It appears this may be achieved by the incorporation of at least three scales of assessment allowing for comparison at different scales in the same habitat.

More study is needed in the selection of scale to be measured. Selection of scale is difficult to evaluate due to differences in habitat at each study site. However, we feel choice of scale should be selected based on at least the following factors. Of primary concern should be the habitat in which the study is conducted. More homogeneous habitats may require a larger number of scales to detect observable differences. Additionally, the behavior of the species being studied must be addressed in selecting the size and number of scales to be assessed. For example, species with large ranges will require large scales to account for greater movement of individuals of these species.

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